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COMPARATIVE HABITAT USE BY LOUISIANA AND NORTHERN WATERTHRUSHES

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Discovering distinctive structural features that characterize the habitats of avian species has been an important goal of researchers (Hespenheide 1971, Noon 1981, Collins 1983). Vegetation structure is frequently thought to predominate in avian habitat selection (MacArthur 1971, Collins 1983), but floristic (e.g., Holmes and Robinson 1981) and physical (e.g., Kendeigh and Fawver 1981) variables can also influence habitat associations.

An additional factor thought to influence habitat use by coexisting, ecologically similar species is interspecific competition. Through competition, species might be expected to diverge in habitat use (Morse 1980). Recent studies, however, suggest that interspecific competition does not always occur between similar species (Morrison 1981, Frakes and Johnson 1982, but see Robinson 1981).

Here, I examine the breeding habitats of the Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes to determine whether their habitats possess distinctive features, and to learn whether overlap in habitat use leads to interspecific competition. Bent (1953) and Eaton (1957, 1958) qualitatively described waterthrush habitats, but there are only limited data (Vassalo and Rice 1982, Swift et al. 1984) concerning the quantitative structure of habitats used by the two species.

STUDY AREAS AND METHODS

Habitats.—I studied habitat use in waterthrushes in northeastern Connecticut from 1978 to 1980 and in 1984, principally in a rocky ravine, Boston Hollow, in Yale Forest, Ashford, Tolland Co. Both species nest in the wooded wetlands extending 1.6 km along the floor of the ravine. In addition, I made qualitative evaluations of habitat at 26 other Connecticut locations.

The wetlands of Boston Hollow have a forest canopy of yellow birch (*Betula lutea*), black ash (*Fraxinus nigra*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), eastern hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*), with conifers predominating in most swamps and deciduous cover predominating along most streams. Speckled alder (*Alnus rugosa*) often reaches sapling size. Shrubs include black alder (*Ilex verticillata*), sweet pepperbush (*Clethra alnifolia*), spicebush (*Lindera benzoin*), and speckled alder. Typical herbs are cinnamon fern (*Osmunda cinnamomea*), sensitive fern (*Onoclea sensibilis*), and skunk cabbage (*Symplocarpus foetidus*).

Morphology.—I identified most individuals in the field by netting and color banding adults. Netted birds were sexed, weighed, and measured (wing chord and tail length). I calculated the relative wing and tail length of each bird by dividing the cube root of body mass, a linear index of body size, into wing and tail measurements.

Habitat structure.—Of 37 territories found at Boston Hollow over four years, I compared habitat data from 10 territories of each species. Because some territories were located similarly to those of previous years and many adults returned to breed in subsequent years, I did not select territories for analysis randomly. Rather, I included as many different sites and individuals as possible to minimize redundancy of observations. Of the 10 Northern Waterthrush territories studied six were overlapped (73–100%) by those of the 10 generally longer Louisiana Waterthrush territories (see map in Craig 1984).

I assessed herb, substrate, and water cover by dividing every territory into five "blocks." In each block I randomly placed a 20-m transect with sampling points every meter (100 total points). At each point I noted the identity of herbs present, presence of moss, type of substrate (mud and leaf litter, rock, root, or log hummock), and occurrence of water. I also distinguished between fast-moving water, which causes surface ripples, and slow-moving water, which does not cause ripples.

I measured shrubs on separate 20-m transects with sampling points every 2 m (50 total points). To estimate crown cover I counted the times shrub species touched a vertical 3-m pole on each of the pole's 1-m sections (Mueller-Dombois and Ellenberg 1974).

To study tree cover, I placed a transect with five points 10 m apart in each of four blocks and measured trees with a minimum height of 6 m and a minimum circumference of 10 cm. For each tree species I calculated an importance value, a relative index of density, frequency of occurrence, and basal area per ha, which provides a measure of proportional representation of forest foliage (Holmes and Robinson 1981). From field data I also calculated trees/ha and mean basal area. I determined sample size for all analyses with Stein's two stage sample (Steele and Torrie 1960).

Because territory sizes differed (Craig 1984), equal sampling effort yielded estimates with different associated variances. For data that were not normally distributed, I used the non-parametric Wilcoxon's two sample test (Steele and Torrie 1960). For the normally distributed morphometric data, I used Student's *t*-test.

RESULTS

Habitats.—At Boston Hollow I found little interspecific difference in total herbaceous cover of territories, and territories of the two species widely overlapped in all features measured (Table 1). In the principal structural classes present, forbs and ferns, territories of Northern Waterthrushes had significantly fewer forbs and significantly more ferns than those of Louisiana Waterthrushes. Lower density of herbs such as *Lycopus, Viola,* and *Sium* resulted in less forb cover, and a much higher density of *Osmunda* was largely responsible for the greater fern cover. A third structural class, coarse herbs (composed solely of *Symplocarpus*), showed no significant interspecific territorial difference. Territories of Northern Waterthrushes had significantly more moss cover than those of Louisiana Waterthrushes.

The ratio of water to ground surface was similar in territories of the two species, as were percent mud and leaves and percent slow-moving water (Table 2). Differences occurred in area of fast-moving water, which was significantly greater in Louisiana Waterthrush territories, and in number of hummocks, which was significantly greater in Northern Water-

Table 1
Percent Herbaceous Cover in Waterthrush Territories

Cover	Louisiana Waterthrush	Northern Waterthrush
Osmunda cinnamomea	6.7 (0–19)[a]	21.4 (2–39)*
Onoclea sensibilis	8.7 (0–27)	10.3 (1–21)
Symplocarpus foetidus	9.2 (0–33)	6.2 (0–37)
Total forbs	17.4 (11–23)	12.5 (4–21)*
Total ferns	17.9 (7–29)	31.9 (12–53)**
Total herbs	40.7 (21–76)	47.3 (30–66)
Moss	19.9 (8–35)	34.6 (5–46)*

[a] Mean with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

thrush territories. Again, territories of the species overlapped in all substrate features measured.

Territories of Northern Waterthrushes had significantly higher total shrub density and higher densities of shrubs in the 1–2 and 2–3 m height classes compared with those of Louisiana Waterthrushes (Table 3). Much of the difference between species was attributable to significantly more evergreens (sapling *Tsuga*) in Northern Waterthrush territories. In contrast, total deciduous density as well as density of individual deciduous species differed only slightly between the species. As in the case of herbs, territories varied widely and much interspecific overlap occurred.

Mean basal area of trees, a measure of trunk size, differed only slightly between territories of the two species, but significantly more trees/ha and a higher evergreen-to-deciduous ratio occurred in the territories of Northern Waterthrushes (Table 4). The importance value (IV) for *Tsuga,* the

Table 2
Percent Cover by Water and Terrestrial Substrates in Waterthrush Territories

Cover	Louisiana Waterthrush	Northern Waterthrush
Fast water	23.7 (5–56)[a]	3.8 (0–13)**
Slow water	22.9 (4–42)	31.6 (14–51)
Hummocks	30.9 (13–48)	45.8 (12–61)*
Mud and leaves	21.5 (3–44)	17.4 (6–61)
Water/ground	1.1 (0.4–2.9)	0.6 (0.3–1.1)

[a] Mean with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

TABLE 3

DENSITY OF SHRUB CROWNS IN WATERTHRUSH TERRITORIES

Substrate	Louisiana Waterthrush	Northern Waterthrush
Ilex verticillata	62.8 (17–106)[a]	95.5 (24–162)
Clethra alnifolia	10.0 (0–23)	19.6 (0–82)
Lindera benzoin	11.2 (0–33)	3.1 (0–9)
Tsuga canadensis	34.6 (0–115)	71.1 (1–106)**
Total deciduous	112.6 (86–166)	136.3 (56–182)
Height classes:		
0–1 m	32.4 (16–59)	28.4 (7–46)
1–2 m	50.6 (31–71)	74.6 (36–116)*
2–3 m	64.2 (21–113)	104.5 (76–153)*
Sum	147.2 (87–210)	207.5 (140–248)**

[a] Mean number of contacts with shrubs on sampling pole, with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

species principally responsible for the differing evergreen-to-deciduous ratio, was also significantly greater in Northern Waterthrush territories, as were IV's for *Alnus*. The remaining common deciduous species showed little interspecific difference, and territories of the species widely overlapped in all aspects of their forest cover.

A comparison of Boston Hollow with qualitatively studied sites in northern Connecticut showed similarities with habitats in steeply hilly regions, but differences with habitats in less hilly central and southern Connecticut. Typical Northern Waterthrush habitats in northern areas

TABLE 4

CHARACTERISTICS OF TREE COVER IN WATERTHRUSH TERRITORIES

Substrate	Louisiana Waterthrush	Northern Waterthrush
Betula lutea	89.5 (60.4–134.4)[a]	70.2 (14.6–104.9)
Acer rubrum	87.8 (55.3–138.9)	77.4 (32.1–173.6)
Alnus rugosa	10.2 (0–37.7)	23.8 (5.4–66.4)*
Tsuga canadensis	56.2 (0–109.0)	106.7 (8.3–164.1)*
Evergreen/deciduous	0.28 (0–0.71)	0.69 (0.04–1.46)**
Mean basal area (m/ha)	253 (176–319)	223 (196–281)
Trees/ha	666 (470–948)	913 (503–1238)*

[a] Mean importance value with range in parentheses (N = 10).
* Species differ at $P < 0.05$, Wilcoxon test.
** Species differ at $P < 0.01$, Wilcoxon test.

TABLE 5
MEASUREMENTS OF WATERTHRUSHES

Species	Wing length (cm)	Tail length (cm)	Mass (g)	Wing/$\sqrt[3]{\text{mass}}$	Tail/$\sqrt[3]{\text{mass}}$
Louisiana Waterthrush					
Male (N = 10)	8.2 ± 0.3[a]	5.3 ± 0.2	20.4 ± 1.2	3.0 ± 0.1	1.9 ± 0.1
Female (N = 7)	8.0 ± 0.2*	5.1 ± 0.1	20.9 ± 0.5	2.9 ± 0.1*	1.9 ± 0.1
Northern Waterthrush					
Male (N = 16)	7.5 ± 0.2	5.2 ± 0.2	16.1 ± 0.6	3.0 ± 0.1	2.1 ± 0.1
Female (N = 11)	7.3 ± 0.3*	5.1 ± 0.3	16.2 ± 0.7	2.9 ± 0.1	2.0 ± 0.1

[a] Mean ± SD.
* Sexes differ at $P < 0.05$, t-test.

were mixed deciduous-*Tsuga* swamps traversed by meandering streams (7 sites). Southern habitats were usually deciduous swamps (4 of 8 sites, one of which had few trees) or dense *Chamaecyparis* swamps (3 of 8 sites). Dense shrub cover was characteristic throughout. Moreover, breeding density was usually highest at mixed or coniferous sites.

The streamside habitats of Louisiana Waterthrushes in northern Connecticut were dominated by mixed deciduous-coniferous growth (8 of 9 sites), but in central and southern regions deciduous forest predominated (7 of 11 sites). The species also occurred along swampy streams (6 of 20 sites). Both species nested in close proximity, although uncommonly, throughout the state (5 of 26 sites).

Morphology.—During this study I measured 10 male and 7 female Louisiana Waterthrushes and 16 male and 11 female Northern Waterthrushes. Tests of wing and tail data suggested that females were slightly smaller than males in both species (Table 5). Females of both species (after egg laying) averaged slightly heavier than males, although not significantly so.

Male and female Louisiana Waterthrushes were significantly larger than male and female Northern Waterthrushes in mass (male: $t = 12.55$, df = 24, $P < 0.01$; female: $t = 14.76$, df = 13, $P < 0.01$) and wing chord (male: $t = 8.68$, df = 24, $P < 0.01$; female: $t = 6.40$, df = 16, $P < 0.01$), but not in tail length (male: $t = 0.17$, df = 24, $P > 0.05$; female: $t = 0.67$, df = 16, $P > 0.05$). Both sexes of the Northern Waterthrush also had greater relative tail length (male: $t = 4.76$, df = 23, $P < 0.01$; female: $t = 2.65$, df = 14, $P < 0.05$) than the respective sexes of the Louisiana Waterthrush, but similar relative wing length (male: $t = 1.90$, df = 23, $P > 0.05$; female: $t = 0.38$, df = 14, $P > 0.05$).

DISCUSSION

Four important differences exist in habitats used by the two waterthrush species at Boston Hollow. Northern Waterthrush territories were more densely vegetated than those of Louisiana Waterthrushes, as indicated by their greater shrub and tree density. They also had more evergreen cover by moss, shrubs, and trees, and possessed typical swamp characteristics such as abundant hummocks, ferns, and alders. In contrast, territories of Louisiana Waterthrushes had more fast-moving water. Despite these differences, the extent of intraspecific variation and species overlap in habitat use was great. Territories of Louisiana Waterthrushes ranged from deciduous-lined rocky streams to heavily coniferous, swampy streams, and those of Northern Waterthrushes ranged from largely coniferous swamps to swampy streams with deciduous cover.

In Connecticut, the habitat shift from north to south appeared largely attributable to a change in habitat availability. Conifers are common only in hilly, higher elevations of northern Connecticut, and deciduous forest dominates in less hilly southern regions (Dowhan and Craig 1976). However, *Chamaecyparis* swamps, which are present mostly in southeastern Connecticut, apparently were preferred by Northern Waterthrushes over the more abundant deciduous swamps. Anderson and Maxfield (1962) considered that deciduous swamps were only recently occupied by Northern Waterthrushes in Massachusetts. This also suggests that coniferous sites are preferred. In view of these observations, the habitats of Boston Hollow seem representative of the range of habitats used in Connecticut, but are more similar to sites used at higher elevations.

The major morphological differences between the two species were that Louisiana Waterthrushes were generally larger and relatively shorter tailed than Northern Waterthrushes. Longer tails theoretically can reduce stalling speed (Pennycuick 1975), and, when combined with lower body mass, this feature should enable Northern Waterthrushes to be more agile than Louisiana Waterthrushes, particularly in the dense foliage found in Northern Waterthrush habitats. This morphological difference may also be related to the greater amount of foraging in vegetation by Northern Waterthrushes compared to Louisiana Waterthrushes (Craig 1984).

The greater evergreen cover in Northern Waterthrush habitats compared to Louisiana Waterthrush habitats may be related to prevailing conditions over the ranges of the species, with conifers predominating in the largely boreal range of Northern Waterthrushes, and deciduous growth predominating over the southeastern piedmont range of Louisiana Waterthrushes. Each species might use such vegetation features as cues in selecting breeding sites (Morse 1980), and hence characteristic habitat associations could persist even where suitable alternative habitats are common.

I cannot explain why Louisiana Waterthrushes seem to prefer streams or why Northern Waterthrushes seem to prefer slow-moving water. Characteristics of the water may simply reflect preferred vegetation features, or they may be related to foraging specializations.

In light of the demonstrated wide overlap in habitat use and my previous findings of considerable overlap in foraging behavior (Craig 1984), the two species appear ecologically similar, at least in Connecticut. They coexist, however, without aggression (Craig 1984), indicating that interference competition is not occurring. The notion that interspecific competition limits ecological similarity, although not without merit (Karr 1983), has sometimes led to alternative explanations being ignored (Wiens 1983).

Evidence of little interspecific competition also comes from recent range expansions by both species. The Northern Waterthrush was unknown as a Connecticut breeder into the early 20th century (Sage et al. 1913; but see Bent 1953 for a 1908 report from coastal Rhode Island), but became well established in Connecticut (Kuerzi and Kuerzi 1934) and Massachusetts (Bagg and Eliot 1937) by the 1930s. Similarly, the Louisiana Waterthrush was formerly common primarily in southern Connecticut (Sage et al. 1913) but since about 1920 has increased in Massachusetts (Bagg and Eliot 1937) and is now found to northern New England (Tingley 1983).

Lack of aggression between similar species has sometimes been attributed to past competition having caused necessary niche partitioning (Noon 1981). The roughly 50 years that the species have been in frequent contact, however, seems a short time for refinement of such niche shifts. Yet, I have observed no interspecific aggression, appreciable behavioral difference (Craig 1984), or consistent habitat segregation by the two species. I therefore propose that habitat use by the Louisiana and Northern waterthrushes can best be explained in terms of independent evolutionary histories and individual ecological requirements.

SUMMARY

Habitat use by the Louisiana (*Seiurus motacilla*) and Northern (*S. noveboracensis*) waterthrushes was studied at Boston Hollow in northeastern Connecticut. Territories of Northern Waterthrushes had significantly greater shrub and tree density, more evergreen cover by moss, shrubs, and trees, and more swamp related features such as hummocks, ferns, and alders, but less fast-moving water than those of Louisiana Waterthrushes. Despite statistical differences, however, both species occupied a wide range of habitats and overlapped considerably in habitat use. The habitats at Boston Hollow seemed representative of the range

of habitats used throughout Connecticut, but were more similar to those used at higher elevations. Both species coexisted without aggression even though they overlapped in habitat use and in territorial boundaries. Observed patterns of habitat use appear best explained in terms of independently evolved ecological requirements of each species.

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LITERATURE CITED

Anderson, K. S. and H. K. Maxfield. 1962. Sampling passerine birds in a wooded swamp in southeastern Massachusetts. Wilson Bull. 74:381–386.

Bagg, A. C. and S. A. Eliot, Jr. 1937. Birds of the Connecticut Valley in Massachusetts. Hampshire Bookshop, Northampton, Massachusetts.

Bent, A. C. 1953. Life histories of North American wood warblers. U.S. Nat. Mus. Bull. 203.

Collins, S. 1983. Geographic variation in habitat structure for the wood warblers in Maine and Minnesota. Oecologia 59:246–252.

Craig, R. J. 1984. Comparative foraging ecology of Louisiana and Northern waterthrushes. Wilson Bull. 96:173–183.

Dowhan, J. J. and R. J. Craig. 1976. Rare and endangered species of Connecticut and their habitats. Conn. Geol. Nat. Hist. Surv. Rept. Invest. 6.

Eaton, S. W. 1957. A life history study of *Seiurus noveboracensis.* St. Bonaventure Univ. Sci. Studies 19:7–36.

———. 1958. A life history study of the Louisiana Waterthrush. Wilson Bull. 70:211–236.

Frakes, R. A. and R. E. Johnson. 1982. Niche convergence in *Empidonax* flycatchers. Condor 84:286–291.

Hespenheide, H. A. 1971. Flycatcher habitat selection in the eastern deciduous forest. Auk 88:61–74.

Holmes, R. T. and S. K. Robinson. 1981. Tree species preference of foraging insectivorous birds in a northern hardwood forest. Oecologia 48:31–35.

Karr, J. R. 1983. Commentary. Pp. 403–410 *in* Perspectives in ornithology (A. H. Brush and G. A. Clark, Jr., eds.). Cambridge Univ. Press, New York, New York.

Kendeigh, S. C. and B. J. Fawver. 1981. Breeding bird populations in the Great Smoky Mountains, Tennessee and North Carolina. Wilson Bull. 93:218–242.

Kuerzi, J. F. and R. S. Kuerzi. 1934. Notes on the summer birds of western Litchfield County, Connecticut. Proc. Linn. Soc. N.Y. 43:1–13.

MacArthur, R. H. 1971. Patterns of terrestrial bird communities. Pp. 189–221 *in* Avian biology, Vol. 1 (J. R. King and D. S. Farner, eds.). Academic Press, New York, New York.

Morrison, M. L. 1981. The structure of western wood warbler assemblages: analysis of foraging behavior and habitat selection in Oregon. Auk 98:578–588.

MORSE, D. H. 1980. Behavioral mechanisms in ecology. Harvard Univ. Press, Cambridge, Massachusetts.

MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley, New York, New York.

NOON, B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51:105–124.

PENNYCUICK, C. J. 1975. Mechanisms of flight. Pp. 1–75 *in* Avian biology, Vol. 5 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

ROBINSON, S. K. 1981. Ecological relations and social interactions of Philadelphia and Red-eyed vireos. Condor 83:16–26.

SAGE, J. H., L. B. BISHOP, AND W. P. BLISS. 1913. The birds of Connecticut. Conn. Geol. Nat. Hist. Surv. Bull. 20.

STEELE, R. G. D. AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York, New York.

SWIFT, B. L., J. S. LARSON, AND R. M. DEGRAFF. 1984. Relationships of breeding bird density and diversity to habitat variables in forested wetlands. Wilson Bull. 96:48–59.

TINGLEY, S. I. 1983. Northeastern maritime region. Am. Birds 37:967–970.

VASSALO, M. I. AND J. C. RICE. 1982. Ecological release and ecological flexibility in habitat use and foraging of an insular avifauna. Wilson Bull. 94:139–155.

WIENS, J. A. 1983. Avian community ecology: an iconoclastic view. Pp. 355–403 *in* Perspectives in ornithology (A. H. Brush and G. A. Clark, Jr., eds.). Cambridge Univ. Press, New York, New York.

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